CAMPTOSTROMA, A LOWER CAMBRIAN FLOATING HYDROZOAN

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A problematic fossil from the Lower Cambrian of Pennsylvania, belonging to the United States National Museum, has been submitted to me for study and description. The material consists of molds only, one specimen showing impressions of the two opposite sides, two others impressions of one side. The incompleteness of the preservation would at first sight discourage a study of the form, but its great age and perplexing appearance invite examination, and the sharpness of the casts permits some fairly conclusive determinations.

The outline of the fossil is broadly elliptic to subcircular, the supposed upper surface slightly convex with a shallow central depression, the supposed under surface flat or slightly concave. The organism was originally either disklike or lenticular—perhaps even a spherical body, the degree of post-mortem compression not being determinable in the fossil state. It is probable that the body was biconvex and relatively soft, as the oblique compression has made a concentric semicircular fold on what I consider the upper surface, with a corresponding ridge on the underside. (See fig. 1.)

No trace of the original substance of the organism is preserved, but a limonite film in the holotype and a silica film in another specimen, between the matrix and the mold of the fossil, suggest the presence of a periderm. The sharp impressions of both upper and under surfaces leave no doubt of the substantial character of the walls and indicate the presence of a surficial skeleton composed of loosely connected spicules, forming the coenenchym. The spicules may have been chitinous in substance, or they may have contained some lime, the form then being comparable to some recent Alcyonacea, as the Xenidae, the spicules of which also contain but a relatively small proportion of lime, or to the Alcyoniidae, in whose soft, fleshy colonies the spicules are not fused.

The fossil suggests at first sight an echinoderm, but the absence of a distinctly plated integument and of mouth and anus is adverse to that view. Neither can a reference to the sponges, which might be suggested by the composition of the body wall of spicules and the presence of numerous openings (possibly inhalant pores), be upheld.

No. 2954.—Proceedings U. S. National Museum, Vol. 82, Art. 13

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There is nothing to indicate the presence of an ostium, and such organs as the monticules also distinguish it from the sponges. Likewise the possibility that this peculiar form might be referable to the Receptaculidae, now considered by some as calcareous algae, is not supported, as the fossil lacks the regular surficial pavement of quincuncial elements so characteristic of those problematical organisms.

All the features of the fossil considered, a reference to the hydrozoans appears most apt. The strange *Paropsonema cryptophya* Clarke from the Naples beds of New York is at once suggested, having in common with our fossil the general outline, possible disklike shape, and concentric ring of radial ribs. *Paropsonema* is now considered as the float or pneumatophore of a large hydrozoan, which in structure resembles the float of *Porpita.* (See Ruedemann, 1916, p. 22.) Another similar fossil is the Ordovician *Discophyllum peltatum* Walcott, considered as a medusa by Walcott but also referred by Ruedemann (*ibid.*) to the Hydrozoa as a probable float of *Siphonophora.* Both *Paropsonema* and *Discophyllum*, while strikingly similar to *Camptostroma* in general features, possess characters that unite them with *Porpita* but that are not found in *Camptostroma. Paropsonema* shows distinct cycles of air chambers and concentric lines, while *Camptostroma*, in the cancellated skeleton and the monticules, possesses characters that are not found, to my knowledge, in any floats of siphonophores but that point distinctly to the Tubulariae.

The central portion of the disklike body on one (upper?) side is marked with numerous large subcircular depressions sunk into a granular surface from which, in some places, faint radiating depressed lines extend, suggesting the astrorhizae of the stromatoporoids. The granular surface in one specimen results from small, closely packed spicules. This area is surrounded by a ring of sharp folds or ribs, the spicules of which are coarser and less closely packed than in the central portion, leaving numerous pores between. These spicules are intermediate between those of the upper central area, the marginal area, and the underside. The ribs fade into the marginal portion and underside, both of which are characterized by a polygonal network of small, widely spaced, vertical, platelike spicules. As a result of this plate arrangement the whole looks like the vermicular, perforate sclerenchyma of numerous stromatoporoids or more recent Hydrocorallinae. In some areas a pavement of short pillarlike spicules appears. The underside is characterized by numerous monticules with depressed centers showing groups of small circular pits and nodes surrounded by radiating trabeculae or tubes (?).

The general form of the bodies, as well as the structure of the cancellated surface of the coenosarc and the monticules, suggesting

zooidal tubes with an interior reticulate columella, finds its closest homology in the Tubulariae, such as the genera *Stoliczkaria* and *Heterastridium* from the Triassic of Europe and Asia. In a somewhat less degree they resemble the Paleozoic Stromatoporoidea, which are currently placed with the Hydrocorallinae and Tubulariae as an early aberrant order, and which are able to form colonial stocks and possess surfaces similar to those of *Camptostroma*.

From both the Hydrocorallinae and Stromatoporoidea this form is separated by its obvious lack of a strongly calcareous coenenchym, although it is quite possible that the zooids of *Camptostroma* had a chitinous periderm and a chitinous, or only slightly calcified, basal coenenchym, as in many recent Tubulariae. The presence of the limonite film in the holotype and of the siliceous film in another specimen between the matrix and the impression of the fossil makes it probable that the polyp stocks were protected by a chitinous outer layer (periderm) as in many recent Tubulariae, and the mold we see is that of the chitinous or slightly calcareous skeleton secreted at the base of the outer layer of zooids or polyps.

From the sharp preservation of the surface features (of the last coenenchym), loss of all interior structure, and the clear evidence of a considerable flexibility and compressibility of the body, I am led to the conclusion that this organism had a chitinous skeleton and resembled most of the present Tubulariae. It may well have been the ancestor of the Stromatoporoidea, which later developed much greater expansion of the coral stocks, which necessitated protection and support by deposition of lime in the skeleton.

As the colonial stock was lenticular if not subspherical, and there is evidence of the presence of only one layer of coenenchym underlying the youngest generation of zooids, it is possible that the earlier and deeper layers of the coenenchym were not preserved, owing to a lack or small percentage of chitin and lime; or it is possible that they were dissolved on further growth and the interior then filled partly with gas (perhaps contained in the mesogloea) and the entire hydrosome was floating. This is by no means improbable for the following reasons: There are floating pelagic colonial stocks or hydrosomes of hydrozoans to-day, as in the family Pelagohydridae and three species of the genus *Margelopsis* (see Hickson, 1909, p. 274). The presence of hydropores on both the upper and under sides of the colonial stock indicates freedom for the zooids to expand on all sides, or a free floating condition of the hydrosome, while the lightness and imperfect development of the skeleton point in the same direction. Finally, there is little doubt among biologists that the mobile habit preceded the sessile and the discovery of the ocean bottom. In the case of this colonial stock, budding would then

have preceded fixation, while the reverse is generally presumed to have happened. (See Raymond, 1921, p. 347.) In the present case, however, the coenenchym layer and the float provided the stratum of fixation for the succeeding generations of zooids, thereby allowing the development of budding. It seems quite logical that this should have been a stage preceding that of discovery of and fixation on the ocean bottom. (See the opposite view of Alexander Agassiz below.) The gradual or accidental sinking of such colonial stocks to a favorable bottom would have provided the transitional stage from the floating colonial stock to the fixed one.

Camptostroma is then to be regarded as an early hydrozoan that had not yet progressed from the pelagic habit to the bottom (benthonic) habit, and was still in the first stages of developing a chitinous (or mucine ?) skeleton.

I have before emphasized on the one hand the striking similarity in outline and coarser sculpture (the ribs) of the disks here described to the floats of the siphonophores, as represented by the recent *Porpita*, the Devonian *Paropsonema*, and possibly the Middle Ordovician *Discophyllum;* and, on the other hand, the close homology of the details of the skeleton of the disk with those of the coenenchym of the Tubulariae. It is of great importance that leading authorities on the Hydrozoa, as Kölliker, Louis Agassiz, McCrady, and Alexander Agassiz (1881, p. 10), have pointed out that the relationship of the Velellidae and Porpitidae to the tubularian hydroids is very close. Agassiz describes very fully how *Porpita* might be derived from a Hydractinia, or *Podocoryne* "in which the chitinous extension of the base of the coenosarc may perhaps be considered as the first indication of the formation of the float" (*op. cit.* pp. 10, 11). He goes even further in indicating the homologies in the zooids of the Tubulariae and the Siphonophora mentioned and (*op. cit.* p. 12) in pointing also to the close relationship of *Porpita* to the Hydrocorallinae, the singular white plate of the float, and its peculiar structure reminding him of the porous structure of the corallum of Sporadopora, Allopora, and Millepora, and finally even in mentioning the Stromatoporae, which, if related to Millepora, would carry back the hydrozoans to the Silurian. Summarizing these observations, it seems safe for us to consider *Camptostroma* as a tubularian hydrozoan with relations to the Siphonophora on one hand and the Paleozoic Stromatoporoidea on the other, to the ancestors of all of which it may stand in close relation through its generalized character. It is to be remembered that tubularian Hydrozoa and Siphonophora apparently were already present in Lower Cambrian time.[1]

[1] I have recently described (1931, p. 2) a Middle Cambrian hydrozoan (*Chaunograptus scandens*) of the campanularid type (order Calyptoblastea).

CAMPTOSTROMA,[2] new genus

Lenticular or spheroidal bodies with chitinous or slightly calcareous skeleton present in only one surficial layer. One (upper?) surface has central circular area with granular surface, and short, subcircular, zooidal tubes, surrounded by primitive astrorhizae. Central area surrounded by a concentric ring of radiating ribs with granular surface. Remaining surface composed of reticulate meshwork of platelike spicules surrounding round pores and larger monticules, with central groups of pores and knobs.

Genotype.—Camptostroma roddyi, new species.

CAMPTOSTROMA RODDYI, new species

FIGURES 1, 2; PLATES 1–4

Description.—Hydrosoma free, lenticular to ellipsoidal or spheroidal in shape, of size of a small apple (largest, diameter 66.5 mm;

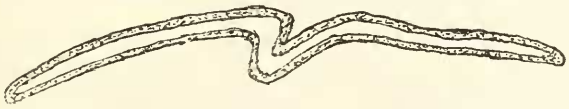

FIGURE 1.—Diagrammatic cross section of the holotype of *Camptostroma roddyi*, showing fold on both the upper and under sides produced by lateral compression

another, incomplete, 45 mm), flexible, probably floating. One side (upper?) possessing a central, circular to elliptic, slightly convex area (33 by 28 mm in type), with depressed center; its surface is granular and perforated by fairly evenly distributed (in quincuncial

FIGURE 2.—Vertical section of *Camptostroma roddyi*, showing the layer of coenenchym with the thecal pores on upper and under sides and monticules on underside. The dotted lines indicate extent of ribs

arrangement) subcircular depressions (many of which have a limonite nodule at the bottom and originally were undoubtedly pores), about 0.5 mm in diameter and 1.5 mm apart. Many of the pores surrounded by somewhat crudely radiate or stellate furrows, suggesting a primitive form of astrorhizae of the Tubulariae (as *Porosphaera*) and Stromatoporoidea.

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[2] Καμπτός, flexible + στρῶμα, layer.

Central smooth areas surrounded by a concentric zone of prominent radiating ribs, about 10 mm long and 1 mm wide, separated by equally wide intervals. Ribbed area possessing granular surface like the central one, but lacking the pores.

The marginal region of the upper side (outside the ribbed area) and the whole under surface composed of short (about 0.5 mm long), straight or slightly curved, vertical, platelike spicules that form a reticulate meshwork with irregular, circular, polygonal, and elongate pores, averaging 0.5 mm in diameter. Where best preserved they are fairly uniformly circular. Between them, in the middle of the underside, are fairly evenly distributed monticules, about 2 mm apart and 1.5 to 2.5 mm in diameter, circular in outline, slightly convex, surrounded by radiating spicules, and often provided with a central group of round knobs and depressions.

One of these specimens was collected more than 10 years ago by Dr. H. Justin Roddy, then at the Teachers College, Millersville, Pa., and now at Franklin and Marshall College in Lancaster, Pa., while the holotype was obtained by him in 1931.

Horizon and locality.—Lower Cambrian, Kinzers formation (*Olenellus* zone): Loc. 12x, Fruitville, 3 miles north of Lancaster, Pa.

Holotype and paratypes.—U.S.N.M. No. 85181.

CAMPTOSTROMA RESSERI, new species

PLATE 3. FIGURES 1–3

Another fossil of similar outline and character—merely an impression in black Lower Cambrian slate from North Granville Bridge, N. Y., found in the National Museum's collections—was later sent to me for comparison with *Camptostroma roddyi.*

The specimen is labeled "medusa imprint?," and indeed at first glance it suggests a medusa more than anything else. The conclusions, however, that were obtained in regard to *Camptostroma* and the presence of a small portion of the original skeleton of the fossil found in the center support the view that this fossil is actually congeneric with *C. roddyi.* I shall therefore describe it as *Camptostroma resseri.*

Description.—Hydrosoma disk shaped or lenticular, of circular outline, about 7.5 cm in diameter. Central area of the side exposed, somewhat elevated and surrounded by a ring of wedge-shaped lobes with flat, smooth surfaces, about 20 mm long and 5 to 7 mm wide at the outer extremity. The outer margin is slightly scalloped corresponding to the lobes. The small portion of the body of the fossil in the center consists of a porous mass strongly resembling slag, and obviously forming the interstitial filling of a meshwork of irregular spicules such as forms the skeleton in the genotype.

Remarks.—The specimen is very incomplete and therefore leaves much to be desired in the evidence for its taxonomic position. Yet the radiate surface sculpture and especially the spongy, porous body in the center clearly place this fossil in the same group with the much better known *C. roddyi.* Likewise the body is too substantial to be derived from a soft medusa; for although found in a much compressed argillaceous slate in which organic remains are completely flattened out, as is *Dactyloidites radiatus*, the impression of this *Camptostroma* reaches 1.6 mm below the surface of the bedding plane along the scalloped margin and twice as much in the central bulge. If there was a corresponding excavation on the other side of the bedding plane, as we must assume, the body reached a thickness of over 6 mm in the shale; certainly a good proof of a solid structure in the living organism such as is indicated by the small patch of meshwork in the center.

Horizon and locality.—Lower Cambrian: North Granville, N. Y.

Holotype.—U.S.N.M. No. 85951.

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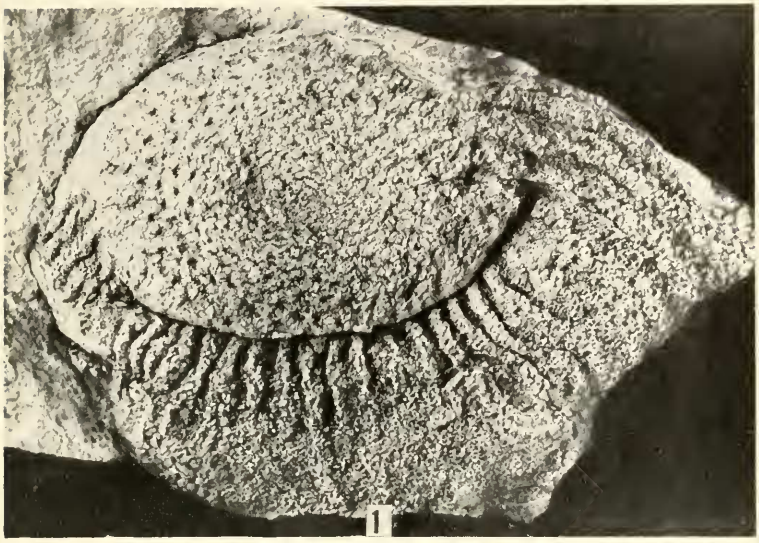
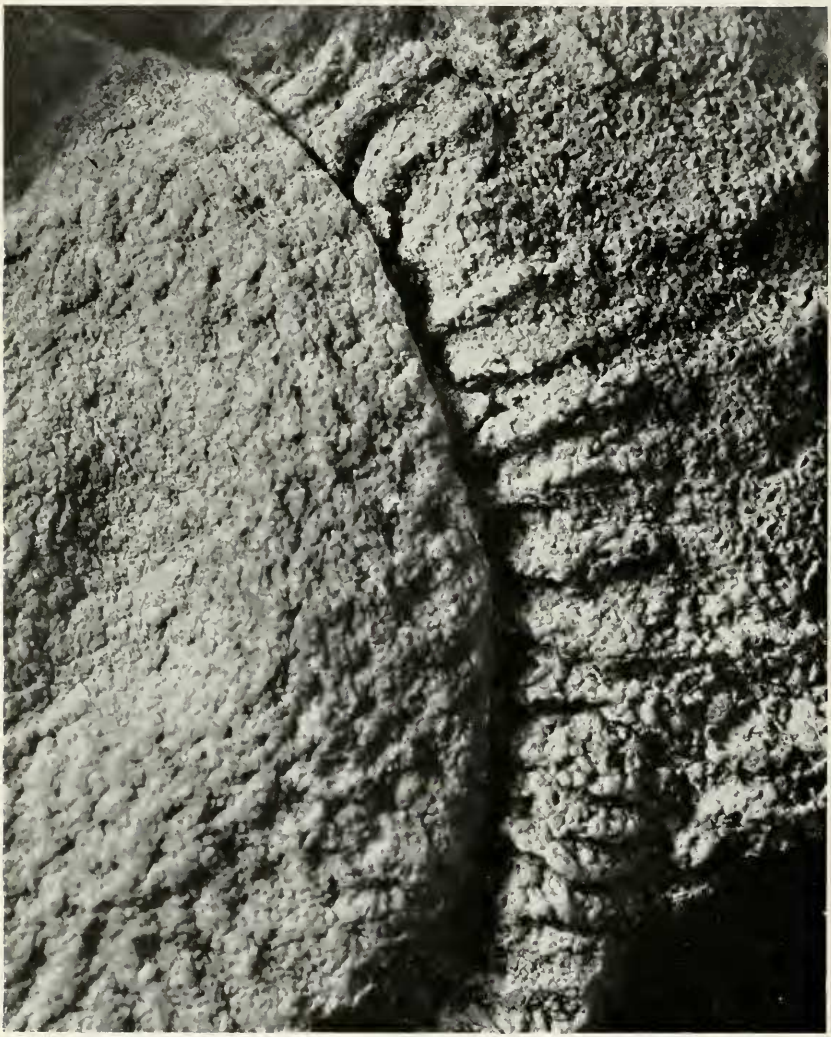


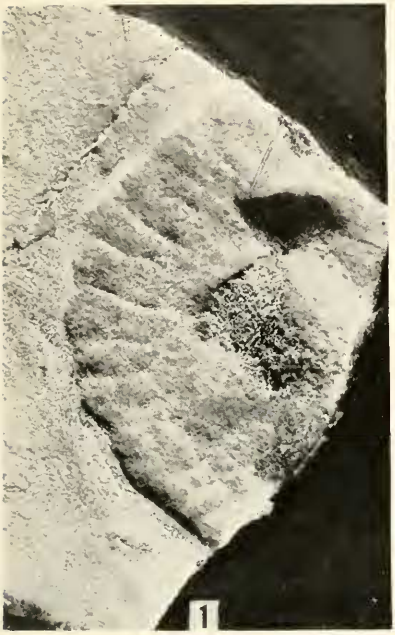
CAMPTOSTROMA RODDYI, NEW SPECIES

1, Dorsal view of squeeze of holotype (× 1½); 2, view of the underside of holotype (× 1½); 3, portion of supposed ventral side enlarged to show monticules (× 8). Lower Cambrian, Kinzers formation (*Olenellus* zone); Fruitville, 3 miles north of Lancaster, Pa.



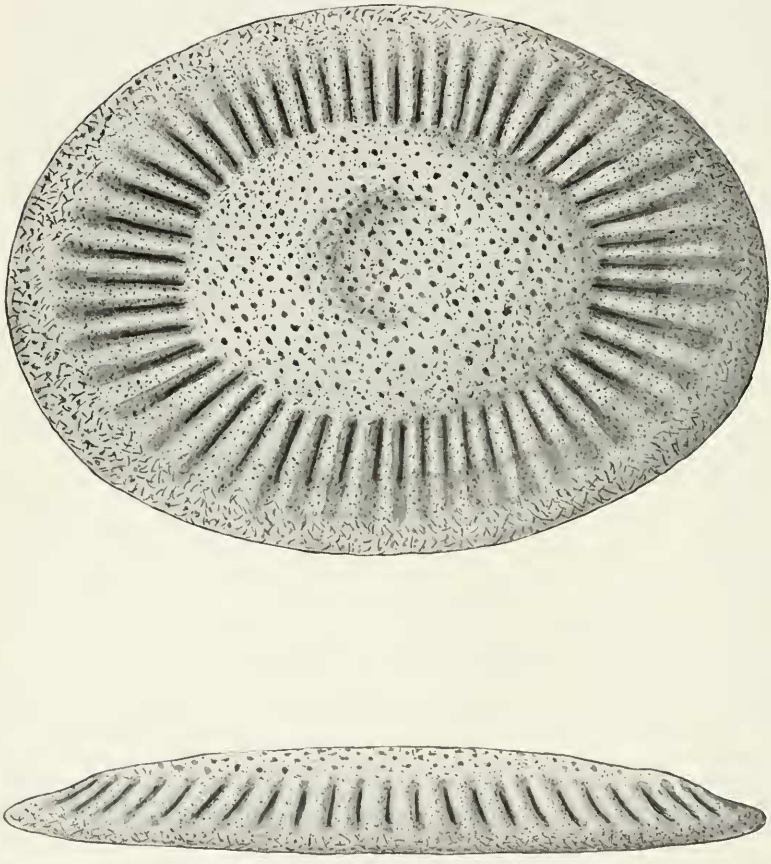
CAMPTOSTROMA RODDYI, NEW SPECIES

View of portion of supposed dorsal surface of holotype showing at the left the central disk, in the middle its outer part with large pores, and at the right the ribbed portion of the animal (× 8). Locality same as Plate 1.



CAMPTOSTROMA RESSERI AND C. RODDYI. NEW SPECIES

1–3, *Camptostroma resseri:* 1, Holotype; 2, enlargement of central portion showing structure (× 8); 3, gutta-percha squeeze of holotype shown in Figure 1. Lower Cambrian: North Granville, N. Y.
4, 5, *C. roddyi:* 4, Another individual exhibiting a thin siliceous film upon which the surface was impressed and which has flaked off in several places revealing the matrix (× 1½); 5, a second rather poor paratype (× 1½). Locality same as Plate 1.



CAMPTOSTROMA RODDYI, NEW SPECIES

Restoration of supposed top surface (upper figure) and of side view (lower figure) of this interesting colony. Locality same as Plate 1.